

WOOD ANATOMY AND CLASSIFICATION OF THE MYRTALES¹

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ABSTRACT

The wood anatomical diversity of the woody Myrtales, comprising Combretaceae, Lythraceae (including Alzatea), Melastomataceae (including Crypteroniaceae), Myrtaceae, Oliniaceae, Onagraceae, Penaeaceae, Punicaceae (can also be included in Lythraceae), Psiloxylaceae, Sonneratiaceae and also Thymelaeaceae, is summarized. All these families share intraxylary phloem and vested pits, and their other wood anatomical attributes represent parts of continuous, sometimes divergent, often parallel, specialization series. Rhizophoraceae, Lecythydaceae, Elatinaceae, Cordiaceae, Chrysobalanaceae and Dialypetalanthaceae are excluded because they lack this combination of characters. The phylogenetic relationships within Myrtales are discussed, and pictured in a two-dimensional diagram (Figs. 2–8). Most families are mutually closely related. The wider wood anatomical affinities of the order are with Gentianales.

Features from vegetative anatomy such as bicollateral bundles and vested pits in the wood have entered discussions on the delimitation and classification of the order Myrtales for a long time. In this paper the entire evidence from wood anatomy will be applied to these taxonomic aspects. The knowledge of the wood anatomy of truly or putatively Myrtalean families has considerably increased in recent years (see references cited under the summarized wood anatomical descriptions) so that a discussion of its taxonomic implications can be meaningful. Our paper cannot, unfortunately, take wholly herbaceous families such as Haloragaceae and Trapaceae into consideration. For a survey of all families that have, from time to time, been assigned to the order Myrtales, the reader is referred to Dahlgren and Thorne (1984).

DELIMITATION OF THE ORDER MYRTALES

All families that have been and are currently regarded as indubitable members of the Myrtales are characterized by a combination of two anatomical features: vestures in the bordered pits of the secondary xylem, and bicollateral bundles in the primary stems (and leaves as far as major bundles are concerned), resulting in the presence of intraxylary or internal phloem in woody stems (not to be confused with interxylary or included

phloem, which occurs in a restricted number of genera and families of the order only). Several authors have also used one or both of these characters in their delimitation of the order.

Vested pits and intraxylary phloem are rather uncommon in the Dicotyledons, as can be seen in Figure 1, where the distribution of these characters is illustrated using Dahlgren's (1980) diagrammatic classification. The data are derived from Metcalfe and Chalk (1950), completed for recent records of vested pits by Meylan and Butterfield (1974), Miller (1977), and Baas and Werker (1981).

The combined occurrence of vested pits and intraxylary phloem appears to be very rare. Outside the Myrtales both features are found only in part of the Gentianiflorae (Apocynaceae, Asclepiadaceae, Loganiaceae pro parte) and in the Thymelaeales (Thymelaeaceae only) of Dahlgren's Malviflorae where the two characters are further only of very sporadic occurrence in the Euphorbiaceae, and then not even simultaneously present in the same genera (Bailey, 1933; Metcalfe & Chalk, 1950). Other combined occurrences are limited to Vochysiaceae (Polygalales) and the single genus *Centropodium* of the Polygonaceae (Polygonales).

The sporadic occurrence of the two features outside the Myrtales as understood by us and Dahlgren and Thorne (1984), and their very con-

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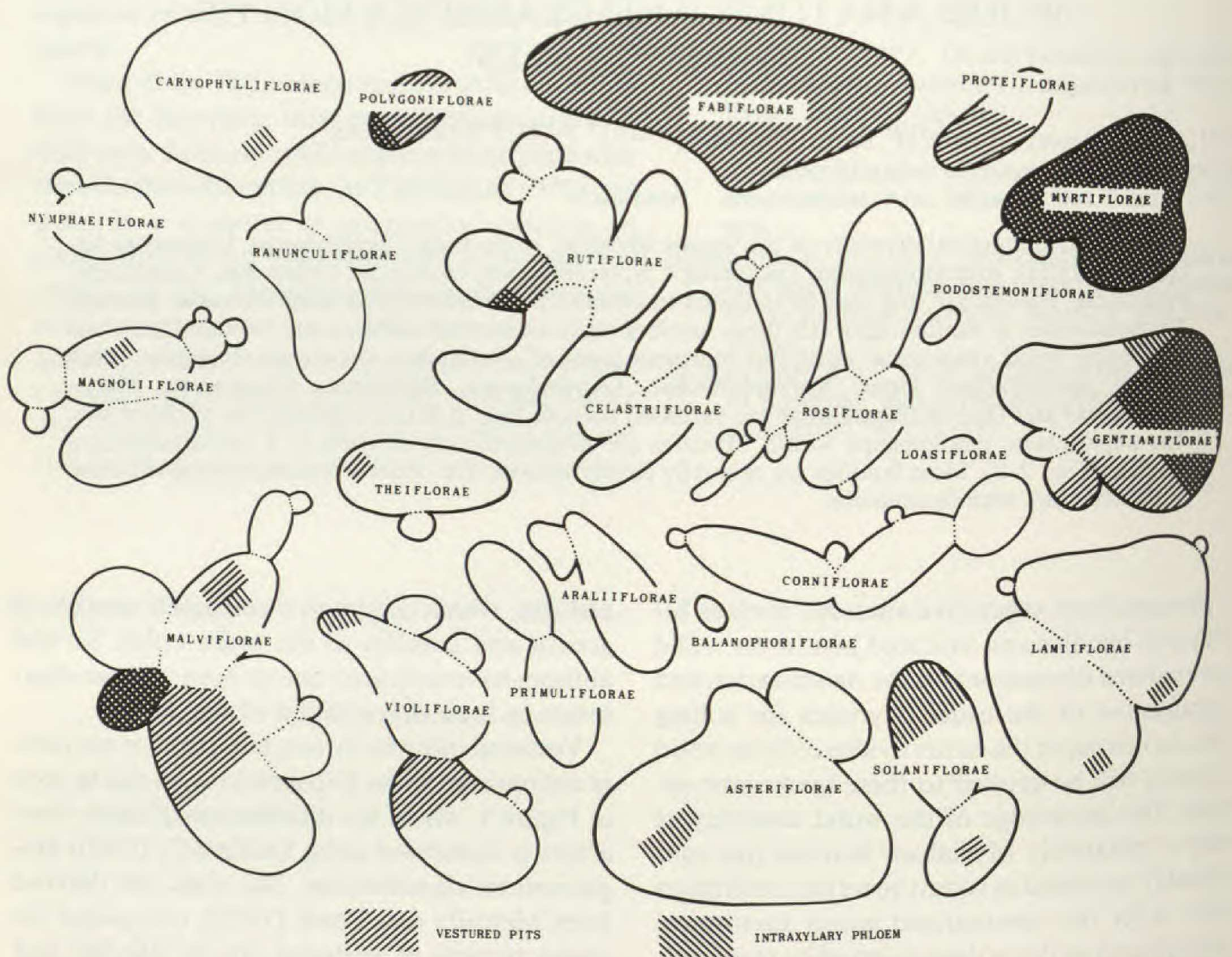


FIGURE 1. Distribution of vestured pits and intraxylary phloem in the Dicotyledons, projected on Dahlgren's classification system (1980). The cross-hatched part of the Malviflorae represents the Thymelaeaceae, in this paper referred to Myrtales.

stant presence within the order, strengthen the value of these characters for the delimitation of the Myrtales. Thus, Rhizophoraceae, Lecythidaceae, Elatinaceae, Cordiaceae, Chrysobalanaceae, Dialypetalanthaceae, Elaeagnaceae and Geissolomataceae, which lack intraxylary phloem and vestured pits, are not considered to belong to Myrtales. The record of vestured pits in Dialypetalanthus by Rizzini and Occhioni (1949) needs confirmation; in a wood sample we studied, vesturing is not obvious, but SEM studies should be carried out to verify this. These families also do not recall true Myrtales in other combinations of wood anatomical features (cf. van Vliet, 1976b, on Rhizophoraceae; Rizzini & Occhioni, 1949, on Dialypetalanthaceae; Carlquist, 1975a, on Geissolomataceae; and family descriptions in Metcalfe & Chalk, 1950, for other families). Thymelaeaceae, incorporated in Myrtales by Cronquist (1968, 1981) but treated in Malviflorae or Malvaneae as a separate

order by Takhtajan (1980) and Dahlgren (1980), do share internal phloem and vestured pits with Myrtales and will later in this paper be compared with the 'core families' of the order. These are: Combretaceae, Lythraceae (including *Rhyncocalyx* and *Alzatea*), Melastomataceae (including *Crypteronia*, *Dactylocladus*, and *Axinandra*), Myrtaceae (including *Heteropyxis*), Oliniaceae, Onagraceae, Penaeaceae, Psiloxylaceae, Puniceaceae (could also be included in Lythraceae, cf. Thorne, 1976; Baas & Zweypfenning, 1979), and Sonneratiaceae.

WOOD ANATOMICAL CHARACTERS OF THE MYRTALES

On the taxonomic level of the order one should not expect to be able to provide a concise wood anatomical diagnosis. Yet the major wood anatomical features will be reviewed in order to paint at least a sketchy portrait of the wood anatomy

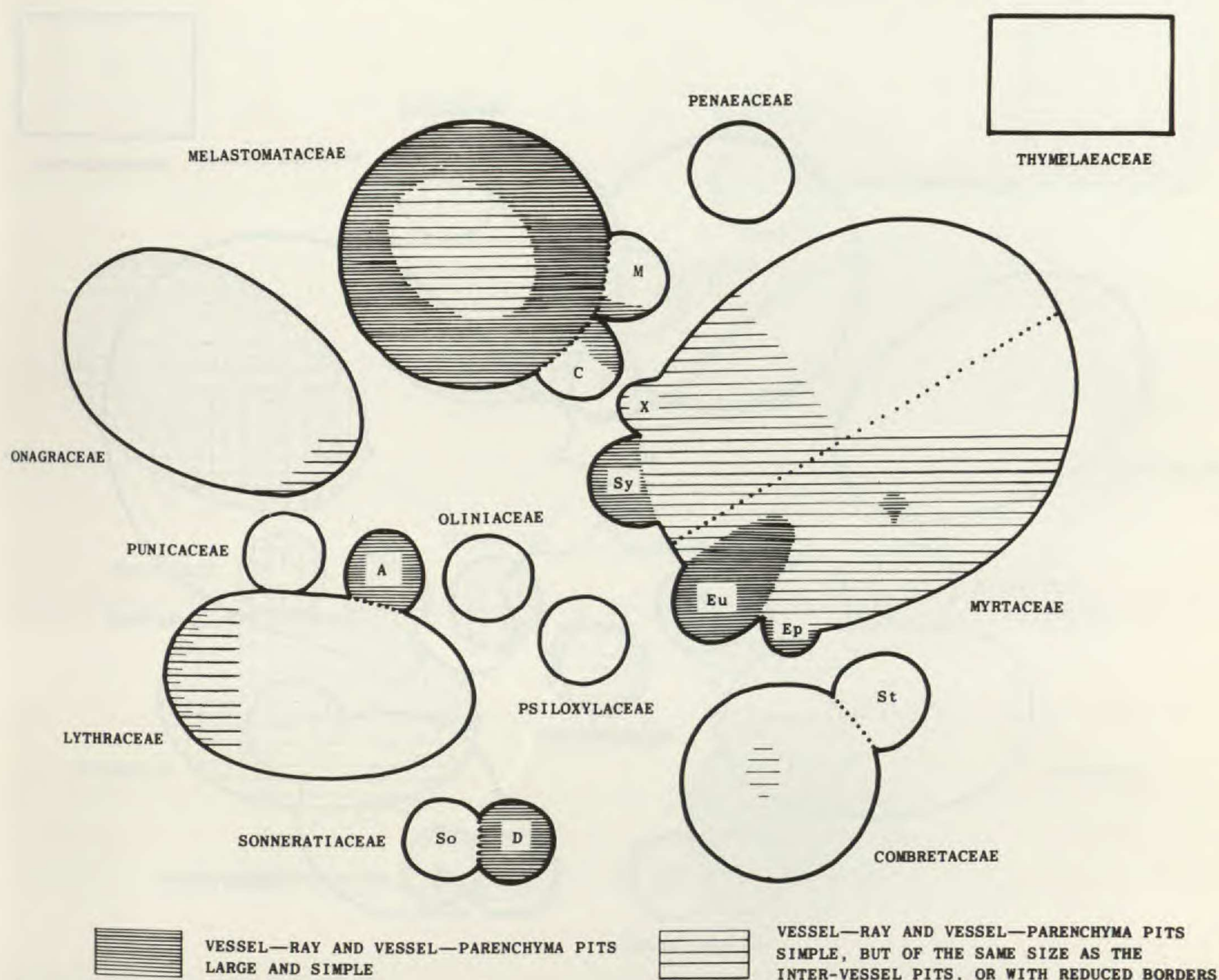


FIGURE 2. Diagram illustrating wood anatomical affinity patterns in the woody Myrtales. Entirely herbaceous families (Trapaceae and Haloragaceae) not considered. Position of Thymelaeaceae uncertain. Distribution of major types of vessel-ray and vessel-parenchyma pits (white areas represent half-bordered pits). A = *Alzatea*; C = *Crypteronioideae*; D = *Duabanga*; Ep = *Eucalyptopsis*; Eu = *Eucalyptus* pro parte; M = *Memecyloideae*; So = *Sonneratia*; St = *Strephonematoideae*; Sy = *Syzygium* sensu lato; X = *Xanthomyrtus*.

of the Myrtales. Thymelaeaceae will not be included in this survey. Constant for the whole order are vested pits and intraxylary phloem as mentioned before. The other characters show various degrees of diversity.

Vessels. A number of Myrtales (most Myrtaceae, Penaeaceae, Memecyloideae of the Melastomataceae, Strephonematoideae of the Combretaceae) have almost exclusively solitary vessels; this feature is always associated with a ground tissue of fiber-tracheids. The other Myrtales have a mixture of vessels solitary and in radial multiples. Perforations are almost always simple except for very few Myrtaceae that have scalariform plates. Inter-vessel pitting is almost always alternate, and if deviating from this type (some Melastomatoideae and Onagraceae), the elongated pits must be considered derived from

the isodiametric alternate pits (van Vliet, 1981; Carlquist, 1975b). Vessel-ray and vessel-parenchyma pits vary widely from half-bordered to large and simple. *Vasicentric tracheids* are typical for most Myrtaceae, and some Combretaceae and Lythraceae show vascular tracheids and/or narrow vessels associated with the normal vessels. *Fibers* either have distinctly bordered pits and are non-septate (fiber-tracheids; see list of Myrtales with solitary vessels above) or more commonly are often septate and have simple to minutely bordered pits confined to the radial walls (libriform fibers). Fiber dimorphism, presumably culminating in parenchyma development (i.e., phylogenetically, *not* ontogenetically) occurs in many Melastomatoideae, some Lythraceae, and weakly in Punicaceae. *Parenchyma* is most typically scanty paratracheal (this type oc-

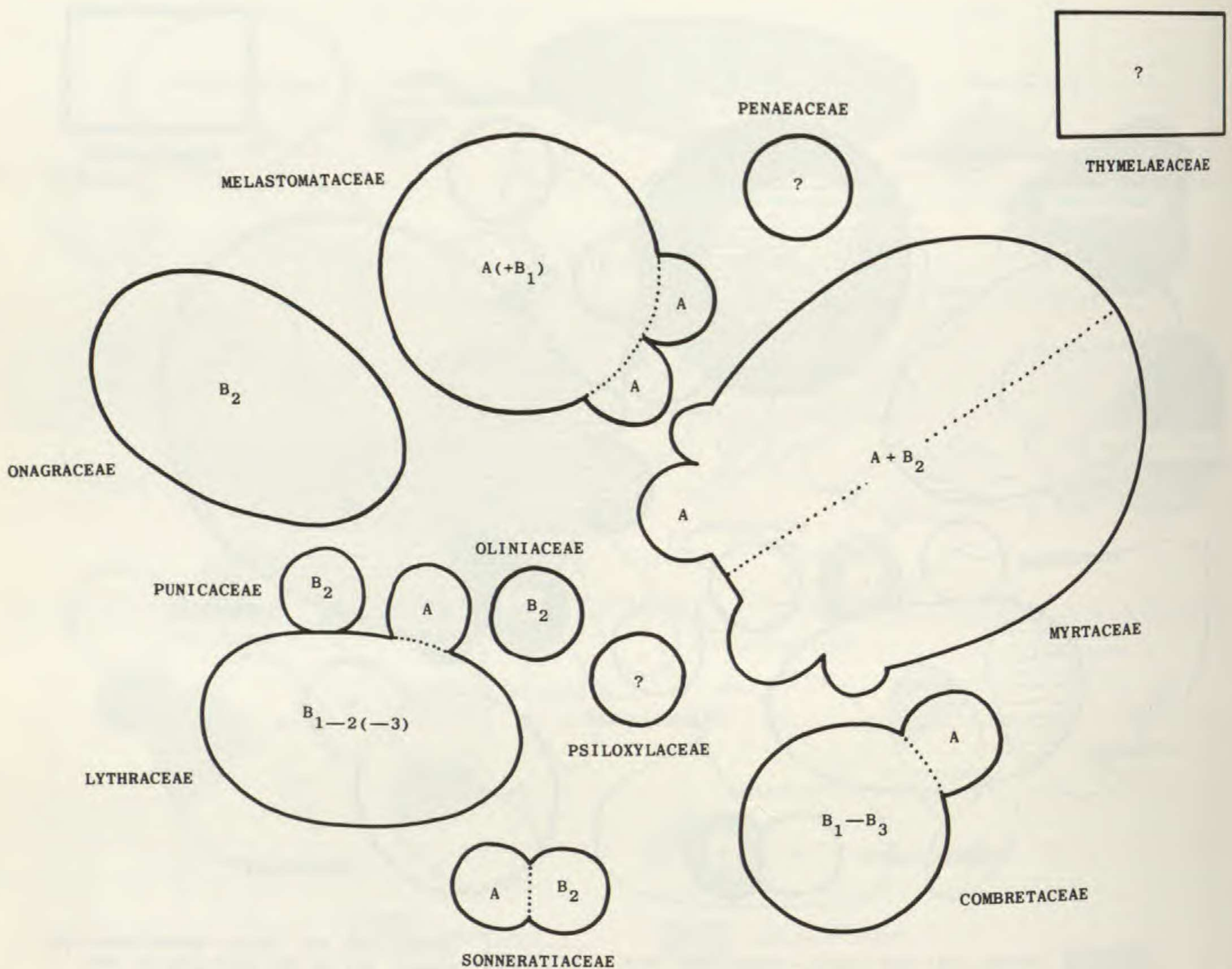


FIGURE 3. Distribution of various types of vestured pits according to van Vliet's classification (1978) in Myrtales. Families not studied are queried. See also legend to Figure 2; in the case of *Alzatea*, A stands for both the genus name and the type of vesturing.

curs in *all* families); in addition, it may be apotracheally diffuse or in narrow, short to continuous broad bands in some representatives; if more abundantly paratracheal it varies from vasicentric, aliform to confluent, to paratracheally banded; most families are heterogeneous with respect to parenchyma distribution. *Rays* also vary, and very often they do not fit into one of the types defined by Kribs (1968), but contain exclusively square to erect cells; in most taxa with heterogeneous ray tissue the central cells are only weakly procumbent. Heterogeneous rays, type I-III and homogeneous rays occur in a minority of genera. The unique feature of radial vessels is entirely restricted to tribe Combreteae sensu van Vliet (1979). Included or *interxylary phloem* occurs in part of the Onagraceae, Combretaceae (Combreteae pro parte) and Melastomataceae (all Memecyloideae sensu van Vliet, 1981). *Crystal types* and distribution are quite diverse in the order and include some unusual forms, which

may be highly diagnostic for some restricted groups. Raphides occur in some Onagraceae and one species of the Melastomataceae. Small elongate to styloid-like crystals occur in some Myrtaceae, Combretaceae and Onagraceae; megastyls occur in one tribe of the Melastomatoideae. Clustered crystals or druses are on record for some Combretaceae, Melastomatoideae, Myrtaceae and Penaeaceae. Rhomboidal crystals are fairly common either in the axial parenchyma or the ray cells; in some Combretaceae, Myrtaceae and Onagraceae they can be large and confined to enlarged idioblasts. Rhomboidal crystals in chambered fibers are typical for a number of Lythraceae, Punicaceae and Psiloxylaceae. Many Myrtales completely lack crystals in their wood. *Silica grains* are almost entirely restricted to part of the Myrtaceae, and are of very sporadic occurrence in the Combretaceae.

Carlquist and Debuhr (1977) included, besides

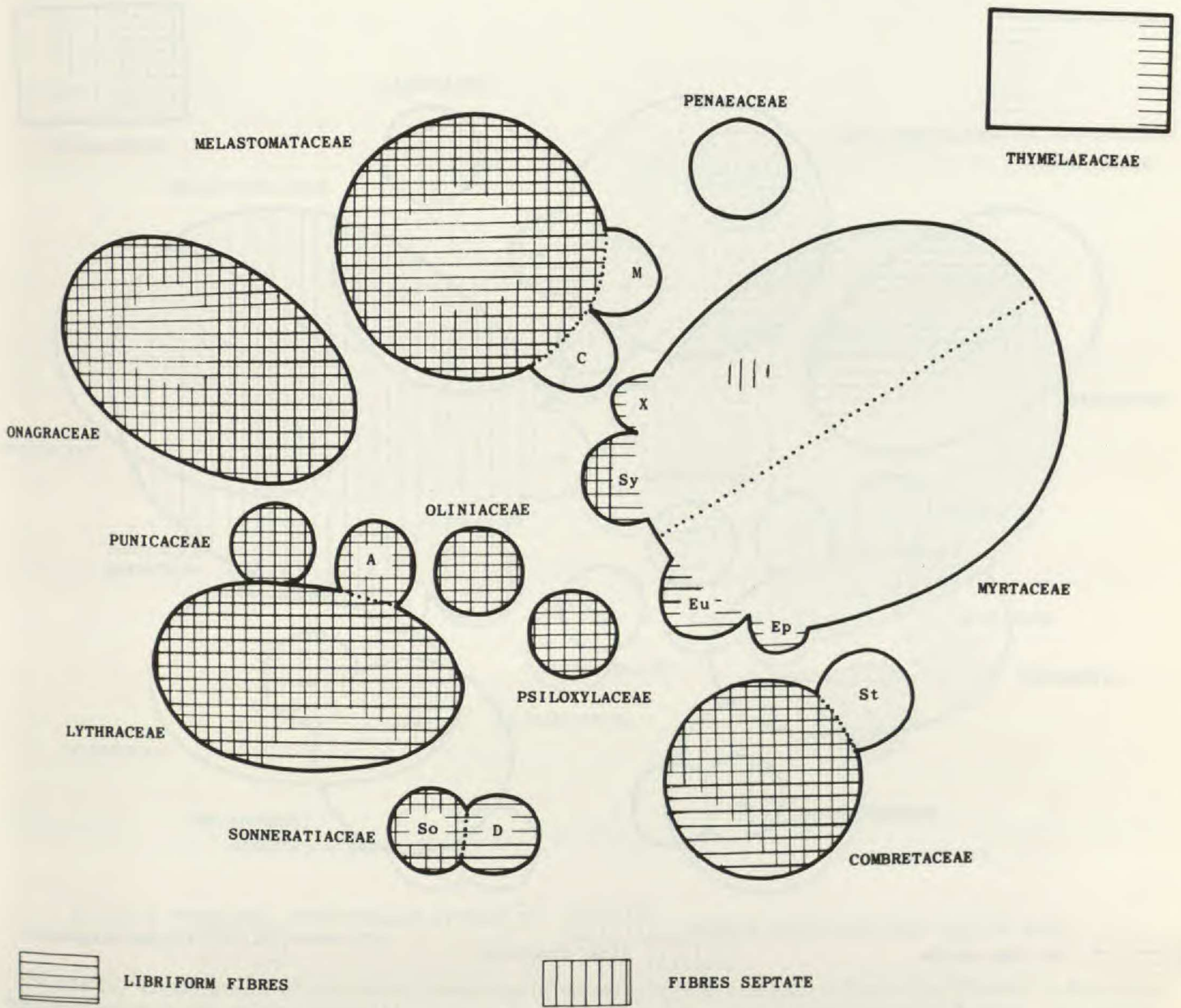


FIGURE 4. Distribution of libriform septate fibers in Myrtales. See also legend to Figure 2.

vestured pits and intraxylary phloem, the presence of crystalliferous strands in axial xylem, in their definition of the order Myrtales. We cannot support this, because so many genera entirely lack crystals, while in some taxa (e.g., *Sonneratia*) crystals are restricted to the ray system. Moreover, one should not equate such diverse types as raphides, styloids, druses and rhomboidal crystals. Presence of amorphous contents in ray cells also cited by Carlquist and Debuhr as a typically Myrtalean feature is probably too aspecific to be useful.

SUMMARIZED WOOD ANATOMICAL DESCRIPTIONS OF THE FAMILIES

(These do not include the common features such as vestured pits, or statements on the absence of unusual features. Type of vesturing is

left out, because of incompleteness of data, but will be discussed in a later section.)

COMBRETACEAE

The two subfamilies Combretoideae and Strephonematoideae are wood anatomically very different, necessitating separate descriptions. For the tribal delimitation of Combreteae as followed here see van Vliet (1979). His Combreteae correspond to the subtribe Combretineae in Exell and Stace's classification (1966; van Vliet, 1976a, 1979).

Combretoideae. Included phloem of the foraminate type restricted to some genera of the tribe Combreteae. *Vessels* diffuse (wood rarely ring-porous or semi-ring-porous), solitary and/or in radial multiples (in Combreteae the normal vessels are mixed with very narrow vessels and

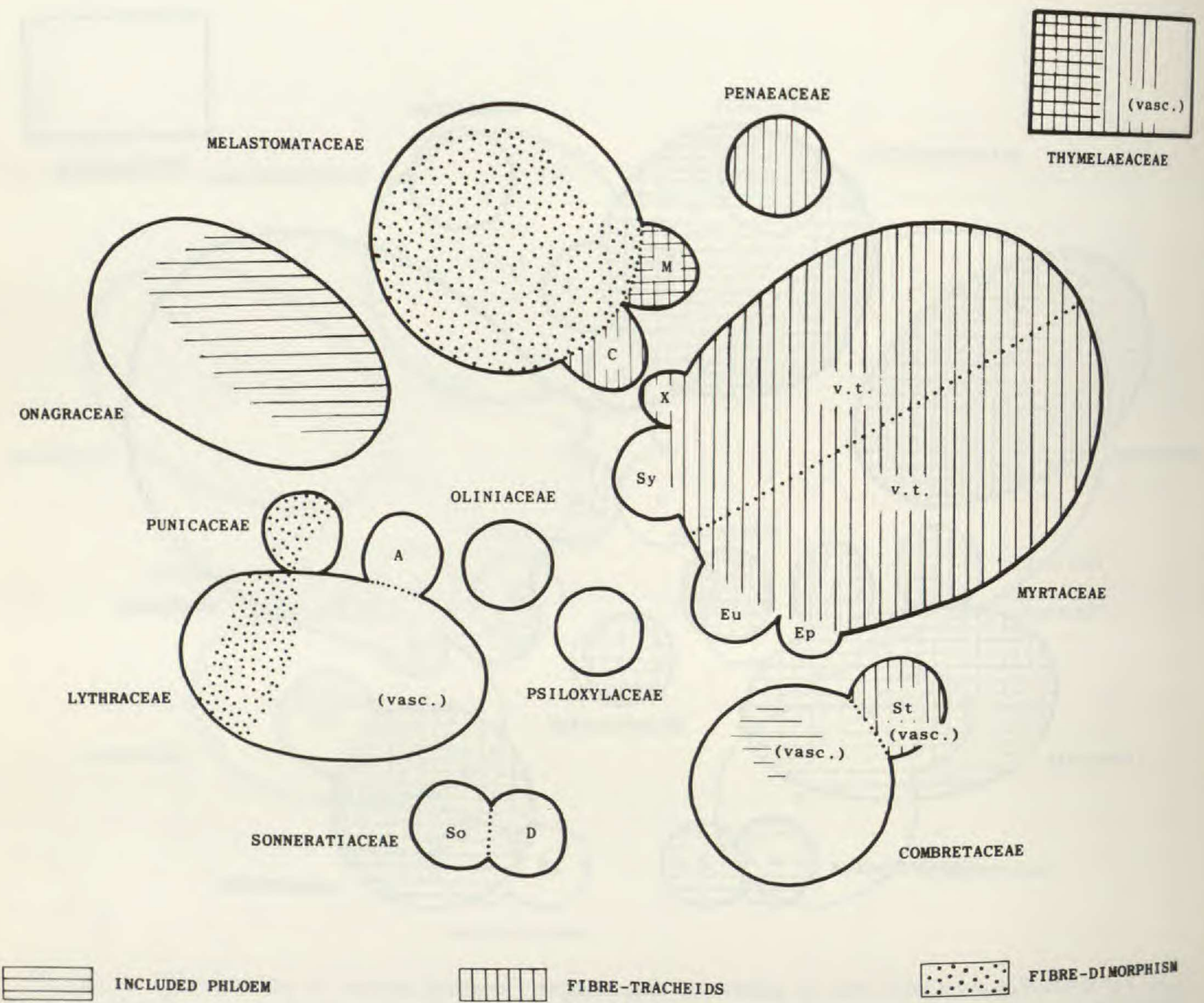


FIGURE 5. Included (interxylary) phloem and various fiber features in Myrtales (cf. Fig. 4). (vasc.) = vascular tracheids occasionally present; v.t. = vasicentric tracheids common. See also legend to Figure 2.

vascular tracheids); average diameter 45–280 μm , average vessel member length 200–650 μm ; perforations simple; inter-vessel pits alternate; vessel-ray and vessel-parenchyma pits mostly half-bordered, but simple in a restricted number of species. Radial vessels (in rays) present in all Combreteae. *Fibers* 500–1,900 μm long, walls with simple pits (libriform), frequently septate. *Parenchyma* often scanty paratracheal only, in part of the genera aliform, confluent or banded and infrequently marginal. *Rays* mostly uniseriate, sometimes 1–3(–more)-seriate, weakly heterogeneous to homogeneous, composed of procumbent and infrequent square cells, infrequently composed of erect and square cells only. *Crystals* variable: small rhomboidal to elongate in axial and ray parenchyma; large rhomboidal completely filling the cells or in enlarged idioblasts of rays and axial parenchyma; rarely styloids; large or small clusters (the latter in idioblasts);

rarely in fibers; absent from some genera. *Silica grains* very rare.

Strephonematoideae. *Vessels* diffuse, mostly solitary; average diameter 250–270 μm , average vessel member length 620–750 μm ; perforations simple; inter-vessel pits alternate; vessel-ray and vessel-parenchyma pits half-bordered. *Vasicentric/vascular tracheids* very rare. *Fibers* 1,760–2,200 μm long, walls with distinctly bordered pits (fiber-tracheids). *Parenchyma* aliform to confluent and in short apotracheal bands or patches. *Rays* heterogeneous II–III. *Crystals* absent. *Amorphous silica* very rare.

LYTHRACEAE

Rhynchocalyx is included in the family description. *Alzatea*, which has been treated in Crypteroniaceae by van Beusekom-Osinga and van Beusekom (1975) but can be accommodated

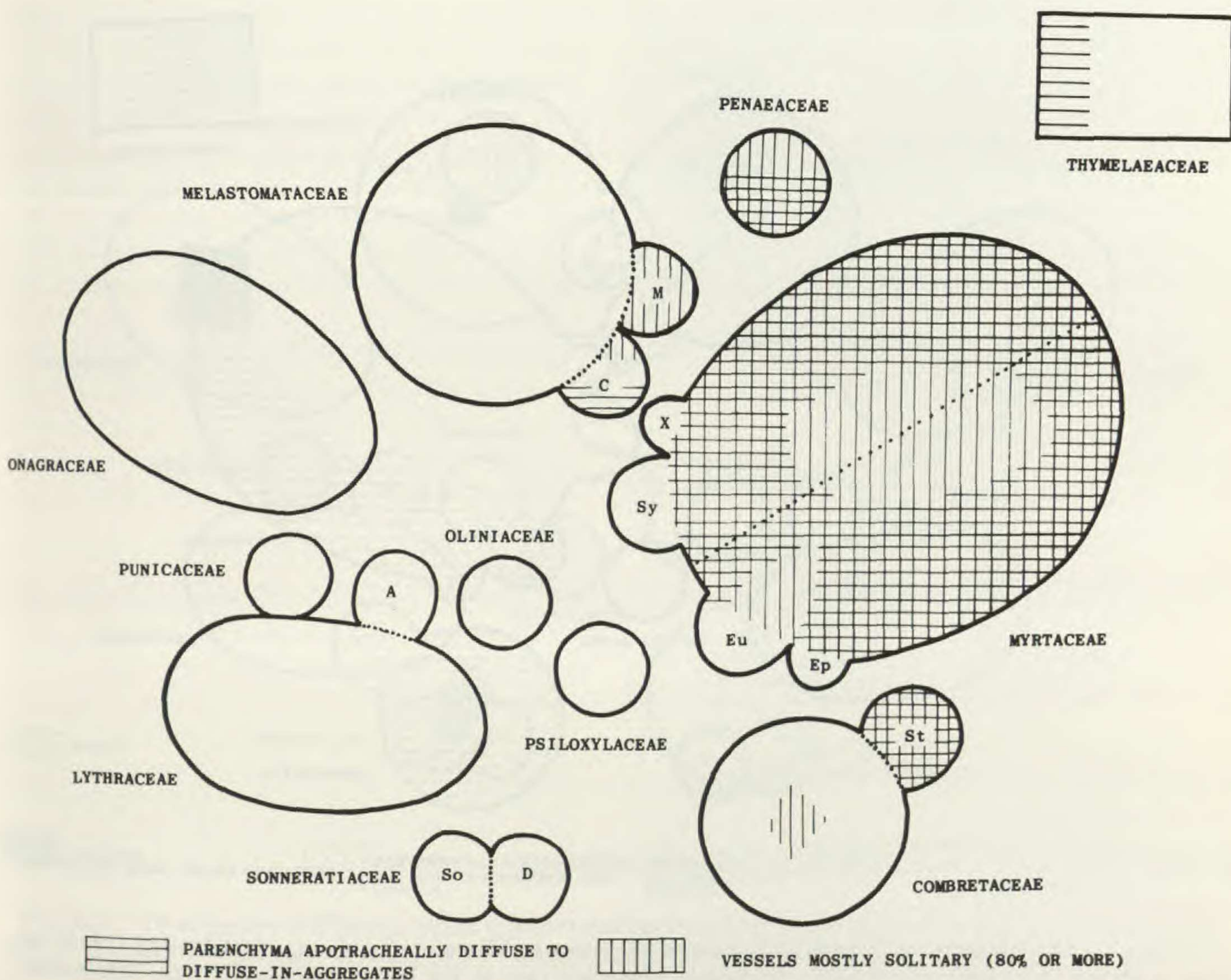


FIGURE 6. Distribution of primitive conditions of vessel grouping and parenchyma distribution in Myrtales. See also legend to Figure 2.

in Lythraceae (Lourteig, 1965; Baas, 1979), possibly merits subfamily status, and its wood anatomical characters are listed separately as far as they deviate from the remainder of the family (Baas & Zweypfenning, 1979; Baas, 1979).

Vessels diffuse (wood rarely ring-porous or semi-ring-porous), frequently in radial multiples; average diameter 30–220 μm , average vessel member length 200–580 μm ; perforations simple; inter-vessel pits alternate; vessel-ray and vessel-parenchyma pits mostly half-bordered, but sometimes simple and fairly large. *Vascular tracheids* very rare. *Fibers* 380–1,350 μm long, walls with simple to minutely bordered pits, frequently septate; in some genera dimorphous with alternating bands or areas of normal and parenchyma-like fibers. *Parenchyma* mostly scanty paratracheal only, rarely apotracheally diffuse, vasicentric or aliform to confluent (and then derived via fiber-dimorphism). *Rays* mostly uni-

seriate (rarely 2–3-seriate), heterogeneous II or composed of erect cells only; rarely homogeneous. *Crystals* rhomboidal in chambered fibers or chambered axial parenchyma strands in part of the family, rarely in ray cells; often entirely absent.

Alzatea. Average vessel member length 730 μm ; vessel-ray pits large and simple; rays 1–3-seriate, heterogeneous I–II.

MELASTOMATACEAE

Three subfamilies with distinctive wood anatomies are recognized: Melastomatoideae, Memecyloideae and Crypteronioideae. The traditionally recognized subfamily Astronioideae has been abolished: *Pternandra* (including *Kibessia*) is transferred to Memecyloideae as a separate tribe; Astronieae (four genera) are transferred to the Melastomatoideae (see van Vliet, 1981). The

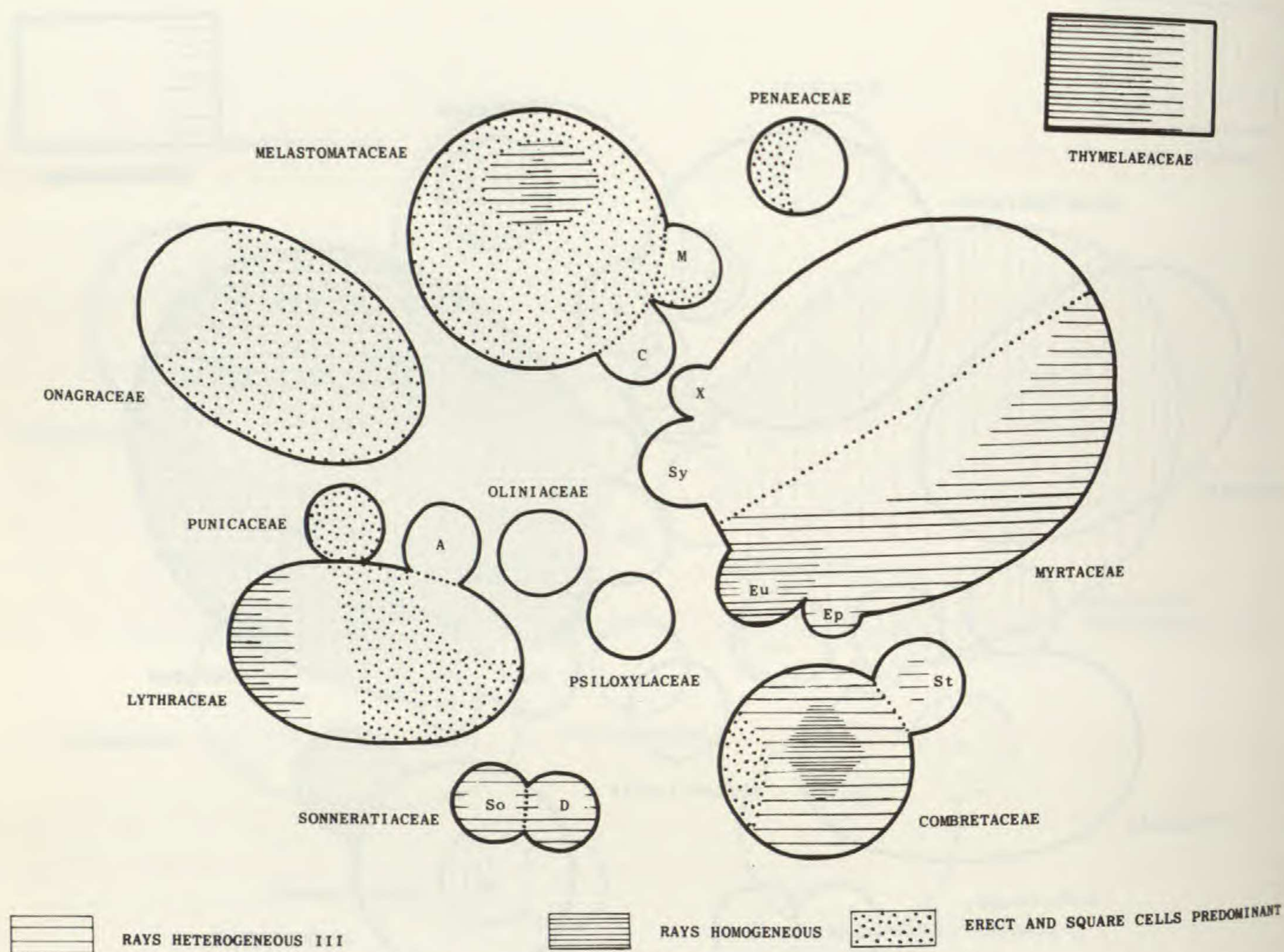


FIGURE 7. Distribution of variously specialized ray types in Myrtales. Krib's ray classification (1968) has been modified to include woods with exclusively uniseriate rays in his Heterogeneous III type. White areas represent more strongly heterogeneous (or heterocellular) rays. See also legend to Figure 2.

Crypteronioideae include *Axinandra*, *Crypteronia* and *Dactylocladus* (van Vliet, 1975, 1981; van Vliet et al., 1981; ter Welle & Koek-Noorman, 1979, 1981; ter Welle & Mennega, 1977).

Melastomatoideae. *Vessels* diffuse, frequently in multiples; average diameter 50–340 μm , average vessel member length 200–1,000 μm ; perforations simple; inter-vessel pits alternate, alternate plus elongate and curved, or scalariform (and then as a derivation from alternate!); vessel-ray and vessel-parenchyma pits mostly simple and large, often in a reticulate or scalariform pattern. *Fibers* 300–1,500 μm long, walls with simple or very minutely bordered pits (libriform), frequently septate and dimorphous: i.e., with parenchyma-like fibers in narrow tangential arcs, or confluent and banded patterns. *Parenchyma* mostly scanty paratracheal, or also apotracheally diffuse within the bands of parenchyma-like fibers; infrequently in continuous bands (and then presumably derived via fiber dimorphism). *Rays* often uniseriate (also 1–7-seriate), mostly com-

posed of erect, square and weakly procumbent cells, rarely homogeneous (i.e., entirely composed of procumbent cells). *Crystals* often absent; raphides present in one species; megastyloids infrequent in one tribe; clustered crystals in idioblasts restricted to species with banded parenchyma.

Memecyloideae. *Included phloem* of the foraminant type present. *Vessels* diffuse, mostly solitary; average tangential diameter 40–120 μm , average vessel member length 250–500 μm ; perforations simple; inter-vessel pits (if present) alternate; vessel-ray and vessel-parenchyma pits half-bordered or simple. *Fibers* 350–1,200 μm long; walls with distinctly bordered pits (fiber-tracheids). *Parenchyma* scanty paratracheal or aliform to confluent and infrequently banded; also associated with included phloem. *Rays* 1–6-seriate, and heterogeneous II–III, or mostly uniseriate and composed of erect and weakly procumbent cells. *Crystals* often absent; large styloids in the included phloem of some species.

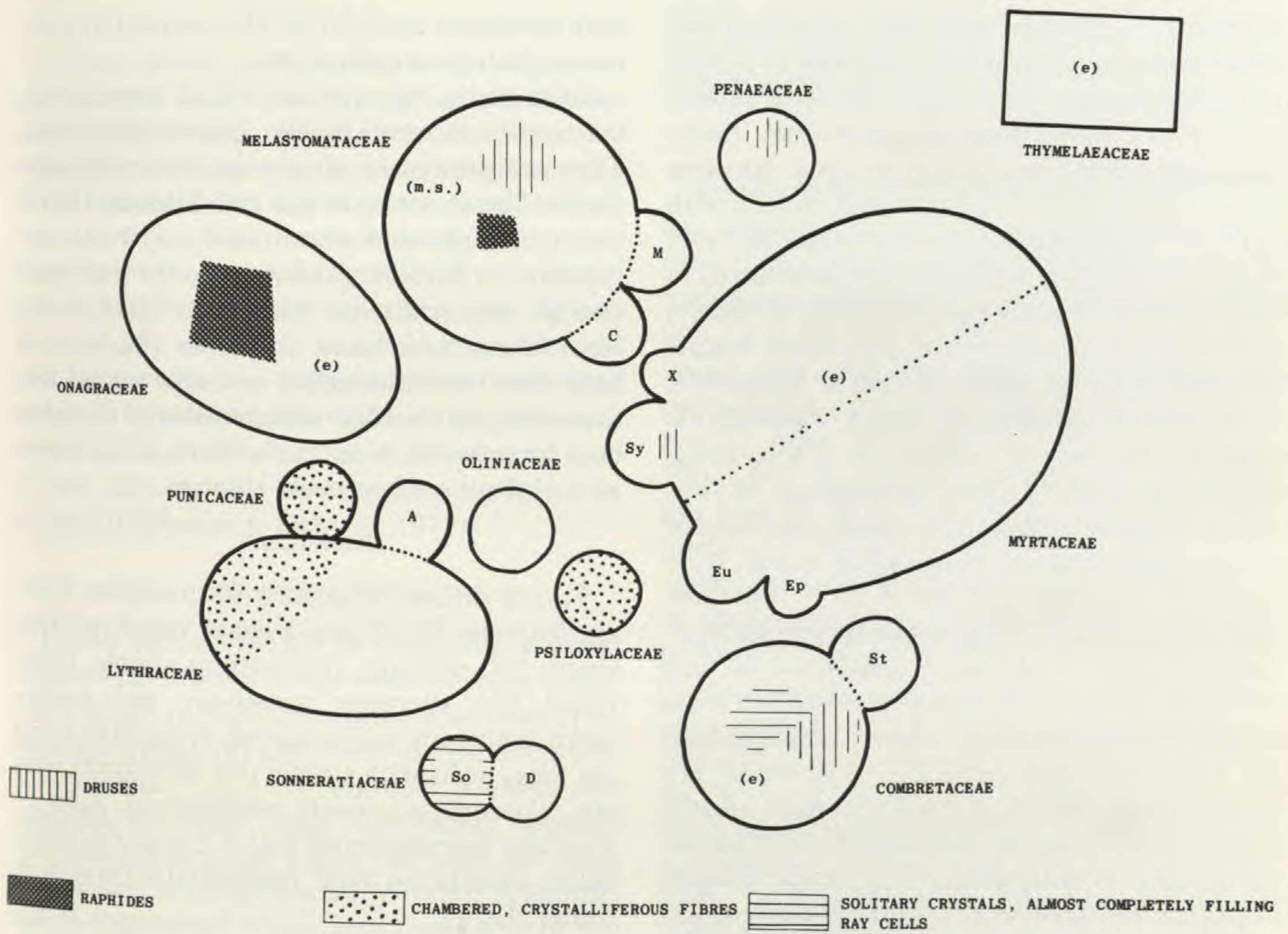


FIGURE 8. Distribution of different crystal types (excluding rhomboidal crystals in ordinary ray or parenchyma cells) in Myrtales. e = elongate crystals; m.s. = megastyloids. See also legend to Figure 2.

Crypteronioideae. Vessels diffuse, solitary and/or in radial multiples; average diameter 80–170 μm , average vessel member length 390–1,120 μm ; perforations simple; inter-vessel pits alternate; vessel–ray and vessel–parenchyma pits half-bordered, rarely also simple. Fibers 600–1,550 μm long, walls with distinctly bordered pits (fiber-tracheids). Parenchyma diffuse in aggregates or aliform to confluent. Rays uniseriate or 1–3-seriate, heterogeneous I or III. Crystals absent.

MYRTACEAE

Combined description of the two traditionally accepted subfamilies Myrtoideae and Leptospermoideae. Schmid (1980) recognized two additional subfamilies: Chamaelaucioideae (formerly in Leptospermoideae) and Psiloxylloideae. For practical reasons the latter is still treated by us as a separate family: Psiloxylaceae (Ingle & Dadswell, 1953; Dadswell, 1972; Metcalfe & Chalk, 1950; supplemented with original observations on slides in the Rijksherbarium collection).

Vessels diffuse, often forming oblique patterns (wood rarely semi-ring-porous), predominantly solitary, but also in multiples in some genera (*Agonis*; *Angophora*; *Eucalyptopsis*; *Eucalyptus* section *Corymbosae* sensu Dadswell, 1972; *Leptospermum* pro parte; *Syzygium* sensu lato sensu Schmid, 1972, i.e., an alliance of genera including *Syzygium*, *Acmena*, *Cleistocalyx* and *Ptilocalyx*, conforming to Ingle & Dadswell's *Eugenia* 'B' complex, 1953, or the *Acmena*-alliance sensu Briggs & Johnson, 1979; and *Xanthomyrtus*); average diameter 30–250 μm , average vessel member length 260–1,090 μm (mostly 400–800 μm); perforations simple, very rarely scalariform (*Neomyrtus*—Butterfield & Meylan, 1974, Meylan & Butterfield, 1978; *Myrceugenia*—Metcalfe & Chalk, 1950, Rudolf Schmid, unpubl. data; *Luma*—original observation, and Rudolf Schmid, unpubl. data; *Ugni*, *Myrteola*, and several other montane and cool temperate genera of Central and South America—Rudolf Schmid, unpubl. data; the record for *Myrtus communis* in Metcalfe & Chalk, 1950, is certainly incorrect); inter-

vessel pits (if present) alternate; vessel-ray and vessel-parenchyma pits half-bordered or simple (sometimes large). *Vasicentric tracheids* mostly present, but absent from *Eucalyptopsis*, *Eucalyptus* pro parte, and *Syzygium* sensu lato (see above). *Fibers* 400–1,500 μm long, mostly with distinctly bordered pits (fiber-tracheids), but with simple to minutely bordered pits (libriform) in *Eucalyptopsis*, *Eucalyptus* pro parte, *Syzygium* sensu lato and *Xanthomyrtus*; very rarely septate (Metcalf & Chalk, 1950; Meylan & Butterfield, 1978; Moll & Janssonius, 1918). *Parenchyma* typically apotracheally diffuse or diffuse-in-aggregates, in addition scanty paratracheal to vasicentric in many genera, more rarely confluent or even in wide or narrow paratracheal bands. *Rays* mostly 1–3-seriate, sometimes up to 8-seriate, rarely uniseriate; heterogeneous II in most Myrtoideae, more rarely heterogeneous I in this subfamily; in Leptospermoideae rays often more weakly heterogeneous to almost homogeneous (in *Eucalyptus* pro parte, *Leptospermum* pro parte, cf. Baas, 1977). *Crystals* if present, mostly small, rhomboidal in chambered axial parenchyma cells in both subfamilies; rarely elongate in slightly enlarged cells; solitary crystals in enlarged idioblasts infrequent in some genera (*Agonis*, *Calycorectes*, *Eugenia* pro parte, *Feijoa*, *Leptospermum* pro parte, *Lophomyrtus* pro parte, *Myrciaria*, and *Nothomyrcia*); druses rare in *Eugenia* (Chattaway, 1955). Crystals always absent from rays. *Silica grains* present in rays of at least 12 genera of the Leptospermoideae (in addition to ten genera mentioned by Ingle & Dadswell (1953), also in *Lindsayomyrtus*, original observation, and *Xanthostemon pachyspermum*, Amos, 1952, a gen. nov. according to Briggs & Johnson, 1979), and rare in two genera (rays of *Osbornia*, parenchyma of *Jambosa*; cf. Amos, 1952) of the Myrtoideae.

Note that within Myrtaceae, *Syzygium* sensu lato and *Xanthomyrtus* (Myrtoideae), together with *Eucalyptopsis* and *Eucalyptus* pro parte (Leptospermoideae), stand out on account of their much higher level of xylem specialization: libriform fibers, vessels in multiples, aliform to confluent parenchyma and large and simple vessel-ray and vessel-parenchyma pits all emphasize this (the two latter features also occur scattered in a few genera). Wood anatomical differences of this magnitude coincide in other Myrtalean families (Melastomataceae and Combretaceae)

with subfamily boundaries, also marked by macromorphological differences.

Silica grains may appear to be of considerable taxonomic interest in the Leptospermoideae. They are present in all genera of the Metrosideros-alliance sensu Briggs and Johnson (1979) so far studied wood anatomically. The only exception is *Kjellbergiodendron*. Interestingly enough this genus has been transferred to the Myrtoideae by Schmid (1980) on the basis of both macromorphological and anatomical features. Outside the Metrosideros-alliance silica has only been found in one suballiance (*Calothamnus*) of the *Leptospermum*-alliance.

OLINIACEAE

Vessels diffuse, frequently in multiples; average diameter 50–70 μm , average vessel member length 500–600 μm ; perforations simple; inter-vessel pits alternate; vessel-ray and vessel-parenchyma pits half-bordered. *Fibers* 900–1,000 μm long, walls with simple pits (libriform), septate. *Parenchyma* scanty paratracheal. *Rays* 1–3-seriate, heterogeneous I–II. *Crystals* rhomboidal in chambered axial parenchyma (Mujica & Cutler, 1974).

ONAGRACEAE

Combined description of the six tribes: Epilobieae, Fuchsiaeae, Hauyeae, Jussiaeae, Lopeziae and Onagreae (Metcalf & Chalk, 1950; Carlquist, 1975b, 1977).

Included phloem of the foraminiate type often present. *Vessels* diffuse, frequently in radial multiples; average diameter 40–110 μm , vessel member length 110–550 μm ; perforations simple; inter-vessel pits alternate, sometimes elongate and curved (in Epilobieae, Fuchsiaeae, Lopeziae, Onagreae pro parte); vessel-ray and vessel-parenchyma pits half-bordered, but sometimes with reduced borders. *Fibers* 240–820 μm long; walls with simple pits (libriform); often septate, or at least nucleate. *Parenchyma* mostly scanty paratracheal, apotracheal bands rare in Hauyeae, apotracheal parenchyma also associated with included phloem. *Rays* uni- to multiseriate, often predominantly of upright cells, or heterogeneous with mostly weakly procumbent and square cells. *Crystals* often as raphides, in axial parenchyma, rarely also in rays or fiber-like cells; sometimes rhomboidal to elongate in non-chambered fibers, and in rays, or absent.

PENAEACEAE

Vessels diffuse, predominantly solitary; average diameter 20–55 μm , average vessel member length 310–890 μm ; perforations simple; inter-vessel pits alternate when present; vessel–ray and vessel–parenchyma pits half-bordered. *Fibers* 380–1,170 μm long, walls with distinctly bordered pits (fiber-tracheids). *Parenchyma* scanty paratracheal and scanty apotracheally diffuse. *Rays* mostly uniseriate and composed of erect and square cells, or 1–3-seriate and heterogeneous II. *Crystals* mostly absent, but present as druses or clusters in chambered parenchyma cells in one species, and as irregular aggregates in another (Carlquist & Debuhr, 1977).

PSILOXYLACEAE

Vessels diffuse, mostly in multiples; average diameter ca. 50 μm , average vessel member length 550–570 μm ; perforations simple; inter-vessel pits alternate; vessel–ray and vessel–parenchyma pits half-bordered. *Fibers* with minutely bordered pits confined to radial walls (libriform), septate. *Parenchyma* typically scanty paratracheal. *Rays* 1–4-seriate, heterogeneous I. *Crystals* rhomboidal, in chambered fibers, very rarely also in ray cells (Schmid, 1980, and original observations; see also Baas & Zweypfenning, 1979).

Note that Schmid (1980) refers to distinctly bordered pits and apotracheal diffuse parenchyma for *Psiloxylon*; in the material at our disposal (Lorence 1488) the pit borders are very small (ca. 1.5–2 μm); apotracheal parenchyma has not been observed and can at most be very infrequent. Our observation of rhomboidal crystals in ray cells is new.

PUNICACEAE

This monotypic family could also be accommodated in Lythraceae (cf. Thorne, 1976; Baas & Zweypfenning, 1979) (Bridgwater & Baas, 1978).

Vessels diffuse, frequently in multiples; average diameter 40–70 μm , average vessel member length 250–330 μm ; perforations simple; inter-vessel pits alternate; vessel–ray and vessel–parenchyma pits half-bordered. *Fibers* 460–540 μm long, walls with simple pits (libriform), septate; tendency to fiber dimorphism observed in several samples. *Parenchyma* scanty paratracheal to virtually absent. *Rays* mostly uniseriate

(rarely up to 3-seriate), composed of erect to weakly procumbent cells. *Crystals* rhomboidal, frequent in chambered fibers.

SONNERATIACEAE

Vessels diffuse, frequently in multiples; average tangential diameter 120–160 μm in *Sonneratia*, 120–230 μm in *Duabanga*, average vessel member length 400–500 μm in *Sonneratia*, 600–800 μm in *Duabanga*; perforations simple; inter-vessel pits alternate; vessel–ray and vessel–parenchyma pits mostly half-bordered in *Sonneratia*, large and simple in *Duabanga*. *Fibers* 700–1,000 μm long in *Sonneratia*, 1,200–1,400 μm long in *Duabanga*; walls with simple pits (libriform); septate in *Sonneratia* only. *Parenchyma* absent in *Sonneratia*, aliform to confluent in *Duabanga*. *Rays* uni(–bi)-seriate, composed of weakly procumbent cells, with occasionally (*Sonneratia*) or commonly (*Duabanga*) square to erect marginal cells. *Crystals* rhomboidal; in *Sonneratia* large and almost completely filling the ray cells; in *Duabanga* smaller and sometimes accompanied by minute crystals in axial parenchyma and ray cells (Metcalf & Chalk, 1950; Venkateswarlu & Rao, 1964, complemented with original observations).

Note that the above data deviate to some extent from those by Venkateswarlu and Rao (1964), which in our opinion is due to some erroneous observations by these authors. Moll and Janssonius (1918) described some form of fiber dimorphism: around some of the vessels the fibers are more thin-walled and have small intercellular spaces between them. This weak form of fiber dimorphism, presumably due to the effect of enlarging vessels on fiber differentiation, should not be identified with fiber dimorphism as occurs in Melastomataceae and some Lythraceae.

THYMELAEACEAE

Included phloem (of the foraminate or concentric type) present in nine genera. *Vessels* diffuse, frequently in multiples, in part of the family in clusters or dendritic patterns; average diameter ca. 30–160 μm , average vessel member length 150–400 μm ; perforations simple; inter-vessel pits alternate; vessel–ray pits half-bordered. *Tracheids* (vasicentric and/or vascular) present in some genera with clustered or dendritically arranged vessels. *Fibers* 300–900 μm long, mostly with distinctly bordered pits mainly confined to

radial walls, but in some genera pits with strongly reduced to almost simple borders. *Parenchyma* scanty paratracheal to vasicentric, or aliform; sometimes also with apotracheal narrow bands or diffuse parenchyma. *Rays* 1-4(-9)-seriate, often almost or entirely homogeneous, sometimes heterogeneous, composed of weakly procumbent central cells and square to erect marginal cells. *Crystals* often absent, if present small, solitary, diamond-shaped, or elongate in ray cells and parenchyma cells; large styloids in included phloem of *Aquilaria*; crystalline masses or crystal sand doubtfully present in few genera (Metcalf & Chalk, 1950; supplemented with original observations on a limited number of genera).

DISCUSSION

Although the previous descriptive sections, partly pictured in Figures 2-8, show a considerable diversity, the order Myrtales as delimited by Dahlgren and Thorne (1984) and us is wood anatomically a fairly closely knit assemblage. The possible inclusion of Thymelaeaceae, the relationship patterns within the order as evident from the wood anatomical variation patterns, and the wider affinities will be the subject of our further discussions.

POSITION OF THYMELAEACEAE

Although treated outside Myrtales by several authors (Takhtajan, 1980; Dahlgren, 1980; Dahlgren & Thorne, 1984), Cronquist (1968, 1981) has advanced arguments to treat Thymelaeaceae as an ordinary member of the order. Wood anatomy tends to support this opinion; apart from the shared intraxylary phloem and vestured pits, there are other similarities. In fact all wood anatomical characters of the Thymelaeaceae can be retraced in the order Myrtales, albeit not in a single family (Figs. 2-8). The occurrence of interxylary (included) phloem in a number of Thymelaeaceae as well as in a number of Onagraceae, Combretaceae and Melastomataceae, is especially significant, because this feature is rather uncommon in Dicotyledons as a whole. The fibers with distinctly bordered pits in Thymelaeaceae are a bit unlike the fiber-tracheids of Myrtaceae, Combretaceae pro parte, Penaeaceae and Melastomataceae pro parte, because the pits are largely confined to the radial walls. The slightly elongate crystals of some Thymelaeaceae recall certain Combretaceae and Myrtaceae. In view of the somewhat reticulate

and faint wood anatomical affinities with the 'core' families of the Myrtales, we would advocate a fairly isolated position, also in view of its other deviating attributes (cf. Dahlgren & Thorne, 1984; Cronquist, 1981). The position of Thymelaeaceae near Euphorbiales and Malvales in the Dilleniidae (Takhtajan, 1980) or Malviflorae (Dahlgren, 1980; Thorne, 1981; Tan, 1980), finds no support in wood anatomy. Vestured pits and included phloem never occur together in the other families of this superorder: vestured pits occur in Dipterocarpaceae and some Cistaceae; their presence in Euphorbiaceae is restricted to Brideliaceae (two genera); intraxylary phloem occurs sporadically in some other Euphorbiaceae and would merit further study to establish whether it is really comparable to the type of internal phloem occurring in Myrtales.

RELATIONSHIPS WITHIN THE MYRTALES

Ideally one would like to construct a phylogenetic system for the Myrtales, based on the occurrence of shared, uniquely derived specializations, as was attempted for Lythraceae (Baas & Zweypfenning, 1979) and Neotropical Melastomataceae (ter Welle & Koek-Noorman, 1981). At the ordinal level, most wood anatomical characters are, however, unsuitable for such a cladistic approach, because of the high probability of parallel specialization lines in individual families. Thus the occurrence of homogeneous rays in some Lythraceae, Melastomataceae, and Combretaceae does not point to mutual affinity across the family boundaries; likewise the specialization series from fiber-tracheids to libriform fibers has probably occurred more than once in the order; even within the family Myrtaceae the occurrence of libriform fibers in the minority of both subfamilies probably represents parallel specialization. The same applies to specialized patterns of parenchyma distribution.

Applying the chiefly unidirectional Baileyan trends for wood anatomical specialization it is, nevertheless, possible to reconstruct the wood anatomy of the putative common ancestor of the Myrtales (cf. Carlquist, 1961, 1962, 1975c, for summaries of and additions to these trends; and Carlquist, 1980; Baas, 1973, 1982, for a discussion of possible reversions). Most primitive character states hypothesized for this common ancestral stock are still represented in a number of extant Myrtales as well as in a fair number of Angiosperm families from other orders. The

combination of ancestral characters can serve as a starting point to discuss the mutual affinities within the Myrtales, as well as the putative affinities with other orders. A wood anatomical diagnosis of 'Protomyrtales' would read as follows:

Vessels mostly solitary, with scalariform perforations (only retained in a few genera of the Myrtaceae) and alternate, vested pits, half-bordered where in contact with rays and axial parenchyma. Vestures of uniform thickness attached to the entire roof of the pit chamber (van Vliet's type A, 1978). Ground tissue of fiber-tracheids. *Parenchyma* scanty paratracheal and apotracheally diffuse. *Rays* heterogeneous I. *Crystals* in axial parenchyma and/or ray cells, probably of several types. *Intraxylary phloem* present.

The following specializations from this ancestral type are evident:

1. Vessels tending to be arranged in (mostly short) radial multiples (most families; cf. Fig. 6 all groups without vertical hatching). This common specialization within the Dicotyledons has probably occurred several times within the order.

2. Vessel-ray and vessel-parenchyma pits with reduced borders to simple, and ultimately large and mostly in a reticulate or scalariform pattern (Fig. 2). This specialization is most evident in Melastomataceae, Myrtaceae pro parte, *Alzatea* and *Lagerstroemia* of the Lythraceae, and *Duabanga* of the Sonneratiaceae; probably at least partly as a result of parallel development.

3. Concentration of vestures around the pit apertures and development of trunk-like bases (van Vliet's series of types A, B1, B2, B3). This hypothetical specialization trend occurs within a number of families and is based on the fact that type A mostly occurs in the representatives that have retained the highest number of primitive attributes in their wood (Strephonematoideae of Combretaceae; *Sonneratia* of Sonneratiaceae; *Alzatea* of Lythraceae; cf. Fig. 3). In Melastomataceae the vesturing is predominantly of type A, and the slightly more specialized type B1 is confined to a few Melastomatoideae—the wood anatomically most specialized subfamily. In Myrtaceae a range from types A–B2 has been encountered, but too few representatives have been studied submicroscopically to relate these types to classification.

4. Reduction of pit borders and limitation of

pits to radial walls in fibers (i.e., shift from fiber-tracheids to libriform fibers) followed by or concomitant with septation of the fibers (Fig. 4). Lythraceae, Sonneratiaceae, Punicaceae, Psiloxylaceae, Onagraceae, Oliniaceae and the largest subfamilies of Melastomataceae and Combretaceae show this specialization; within Myrtaceae it occurs isolated in the two major subfamilies. Fiber dimorphism represents a further specialization, and is limited to part of the Lythraceae, Melastomatoideae and Punicaceae.

5. Parenchyma specialization (quite possibly reversible), presumably followed three different courses: a. *Reduction leading to exclusively very scanty paratracheal parenchyma, or total absence of parenchyma* (most families, notably Melastomataceae, Lythraceae, Onagraceae, Punicaceae, Psiloxylaceae, Oliniaceae, *Sonneratia* of Sonneratiaceae and Thymelaeaceae pro parte). b. *Increase of paratracheal parenchyma* (often paralleled by a decrease in apotracheal parenchyma). This specialization is evident in part of the Myrtaceae, Combretaceae, Crypteronioideae and Memecyloideae of the Melastomataceae, *Duabanga* of the Sonneratiaceae and to some extent in *Pemphis* and *Rhynchochalyx* of the Lythraceae, *Hauya* of the Onagraceae, and some Thymelaeaceae. c. *The presumed development of banded parenchyma through fiber dimorphism* in *Lagerstroemia* pro parte of the Lythraceae and some members of the Melastomatoideae.

6. Ray specialization also occurred along diverging lines: a. *Towards a higher proportion of procumbent cells, and greater procumbency of the marginal cells* (i.e., the classical specialization series according to Kribs, 1935, modified in 1968): Heterogeneous I–II–III–Homogeneous. The homogeneous (or rather homocellular) end station is represented by few Myrtales only, least infrequently in Myrtaceae and Combretaceae, abundant in Thymelaeaceae (Fig. 7). b. *Perpetuation of juvenile ray features* (i.e., composed of square to erect cells, or with only very weakly procumbent cells) *in mature xylem*. This phenomenon of pedomorphosis (Carlquist, 1962) is especially common in Melastomataceae, Onagraceae, Lythraceae and Punicaceae. Penaeaceae and Combretaceae also show this feature in some species but here it is not certain whether this should be ascribed to the truly juvenile nature of the material studied. In the former families many species also never develop substantial amounts of wood, but some representatives at least do show the juvenilistic tendencies in their

rays at the periphery of thick trunks. Carlquist (1962) developed the hypothesis of pedomorphosis to explain the wood anatomical syndromes in a number of woody plants such as giant lobelias and senecios that have probably evolved from a herbaceous ancestry. For the Myrtales involved, such 'secondary woodiness' is not necessarily indicated—the perpetuation of juvenile characters throughout the development of secondary xylem may also be hypothesized for basically woody plants (cf. Baas, 1982). c. *Reduction of ray width* of the originally 1–4-seriate rays to uniseriates (most families), or *sporadically phylogenetic increase in ray width* (partly recapitulated in ontogeny) in e.g., some scandent Melastomataceae.

7. Origin of interxylary (included) phloem in Memecyloideae, Combretaceae pro parte, Onagraceae pro parte and Thymelaeaceae pro parte probably independently of each other (Fig. 5).

8. Miscellaneous specializations: a. *Origin of radial vessels in the rays* of one tribe of the Combretaceae. b. *Development of vasicentric tracheids in Myrtaceae*. This possibility might be questioned. In view of the numerous primitive wood attributes of the Myrtaceae one might also hypothesize that vasicentric tracheids belong to the set of ancestral characters of the Myrtales, and that this feature (like scalariform perforation plates) was lost in all families except one. c. *Development of vascular tracheids* (reduction of very narrow vessels) in some Lythraceae, Combretaceae and Thymelaeaceae (Fig. 5). d. *Development of chambered crystalliferous fibers* (Psiloxylaceae, Lythraceae pro parte and Punicaceae) (Fig. 8). e. *Development of megastyloids in some Melastomataceae*, possibly from an ancestral type with rhomboidal to elongate crystals. It is very difficult to picture the other crystal types as primitive or specialized. Raphides, which represent a highly complex type of calcium oxalate deposition, are restricted in distribution in the Dicotyledons: among the 26 families listed by Metcalfe and Chalk (1950) are some primitive families (e.g., Dilleniaceae and Monimiaceae); in Monocotyledons raphides are more common. One can hardly imagine that in Onagraceae this feature evolved 'de novo' as a new specialization; it seems more likely that the expression of such a presumably old character in derived families is still triggered by unaltered genotypical information. The lack of raphides does not imply that the information is absent but that perhaps it is incomplete or blocked by other genes; such a hy-

pothesis would also be compatible with the 'stray' occurrence of raphides in one *Bredia* species of the Melastomataceae (van Vliet, 1981). By the same token, the haphazard occurrence of elongate crystals or druses (Fig. 8—rare features in the wood of Dicotyledons) might still witness (ancient?) links between the families sharing them in some of their species.

The distribution of some of the primitive and derived character states discussed above over the different families of the Myrtales is given in Figures 2–8; in fact the arrangement of the families is the result of these wood anatomical distribution patterns. There appears to be a high degree of correlation of primitive characters in some of the families or subfamilies and of derived characters in the remaining ones. Primitive characters like solitary vessels, fiber-tracheids, and apotracheal parenchyma occur together in the majority of Myrtaceae, in Strephonematoideae of the Combretaceae, Memecyloideae, Crypteronioideae pro parte, and Penaeaceae. In all these groups, at least part of the species show heterogeneous rays with a clear distinction between the procumbent, central cells and square to erect marginal cells in one to several rows. The most primitive wood anatomical feature of the order, scalariform perforations (few Myrtaceae), coincides with these other primitive features. As far as is known, the presumed primitive type of vesturing also occurs relatively frequently in these taxa. Thymelaeaceae share primitive fibers, and to some extent parenchyma distribution, but are generally more specialized in vessel grouping and ray type.

Although the common retention of primitive features is not a sound basis for postulating close phylogenetic affinity, the above taxa still retain many of the ancestral characters of the Myrtales, and evince at least common ancestry.

From the above it automatically follows that the opposed, specialized character states (vessels in multiples, libriform fibers (mostly septate), reduced or abundant paratracheal parenchyma) also show a high degree of correlation in the remaining taxa: Combretaceae of the Combretaceae, Sonneratiaceae, Lythraceae, Punicaceae, Oliniaceae, Psiloxylaceae, Onagraceae and Melastomatoideae of the Melastomataceae. The incidence of specialized rays (heterogeneous III to homogeneous, and juvenilistic rays) is relatively high in these families, as is the occurrence of the more derived types of vesturing (types B1–3). Within the Myrtaceae, *Syzygium* sensu lato,

Xanthomyrtus, *Eucalyptopsis* and *Eucalyptus* pro parte share the high specialization level of the above mentioned families.

Of these wood anatomically specialized core families of the Myrtales, Psiloxylaceae, Oliniaceae, and some Lythraceae (notably *Alzatea*) have retained a low level of specialization in their rays (heterogeneous I). Especially the wood of *Psiloxylon* and *Olinia* (half-bordered vessel-ray pits) probably resembles that of the ancestor that gave rise to the diversely specialized types in this part of the order (the 'Protolythraceae' type of Baas & Zweypfenning, 1979). Lythraceae and Punicaceae can be directly linked to this type, especially to *Psiloxylon*, through the shared crystalliferous fibers.

Of Sonneratiaceae, especially *Sonneratia* still retains many ancestral features but shows minor specializations in its uniseriate rays and (almost?) total absence of axial parenchyma; *Duabanga* diverged wood anatomically into another direction (aliform to confluent parenchyma, large and simple vessel-ray pits, homogeneous rays) and has a much higher specialization level. Onagraceae could also be derived from this type, but acquired (and/or retained) features that tend to underline a somewhat isolated position such as included phloem, rod-like crystals with one indented and one pointed end (Carlquist, 1975b), and raphides.

For Combretaceae and Melastomatoideae the story is more complex; these taxa belong to families that also have representatives with the primitive Protomyrtalean wood anatomical syndrome. If Combretaceae and Melastomataceae are monophyletic families, this implies that the specialized wood anatomies in the majority of their representatives arose independently from a more primitive type than that represented in the Protolythraceae type, and that the specialized Combretaceae and Melastomataceae are not so closely related to, for instance Sonneratiaceae and Lythraceae, respectively, as their wood structure would suggest. For Combretaceae this is quite acceptable, because the family does not resemble Sonneratiaceae so strongly. For Melastomataceae and Lythraceae it implies that many striking similarities are a result of parallel or convergent development (fiber dimorphism; large vessel-ray pits in most Melastomatoideae and part of the Lythraceae, notably in *Alzatea* and *Lagerstroemia* pro parte; juvenilistic rays; etc.). Parallel developments are more likely to occur in closely related (i.e., genetically similar) groups; the sim-

ilarities in wood structure resulting from parallel or convergent evolution may thus still witness affinities: it seems therefore plausible to hypothesize a direct derivation of the 'Protolythraceae' type from the immediate precursor of Melastomataceae (which must have been very similar, if not identical, to the Protomyrtales type giving rise to Myrtaceae, Penaeaceae, and Combretaceae).

The arrangement of Myrtalean families in the diagrams of Figures 2–8 reflect our conclusions on natural affinity as far as is possible in a two-dimensional system. The deviating position and shape for Thymelaeaceae is not only a reflection of its presumed isolated position, but also of our more limited understanding of this family, simply because we did not study enough representatives in sufficient detail. The arrangement of the woody 'core' families is based on a combination of phenetic and phylogenetic classification principles; more emphasis on phenetic similarities, e.g., the shared possession of interxylary phloem, would put Combretaceae, Melastomataceae and Onagraceae much closer to each other, but, as explained above, the acquisition of this character presumably occurred more than once in the evolutionary history of the order. However, the great distance between Combretaceae and Melastomataceae in our diagram is primarily the result of our priority to put Strophonematoideae near Myrtaceae and Combretaceae near Sonneratiaceae; and not because we consider the two families as mutually remote. Although the diagram is inspired by wood anatomical characters, evidence of other characters (micro- and macromorphological) have also played a role. This is expressed in the adopted family delimitations for Combretaceae, Melastomataceae and Sonneratiaceae, for which wood anatomy could support the splitting of each into two or three separate families. Likewise, the perfect fit of *Psiloxylon* and *Olinia* wood with Lythraceae, has not resulted in the submerging of these genera in Lythraceae in view of evidence from other characters; e.g., the secretory cavities of *Psiloxylon*, which suggest Myrtaceae, as strongly advocated by Schmid (1980).

The splitting of the order Myrtales sensu lato into Lythrales and Myrtales as suggested by Briggs and Johnson (1979) cannot be supported by wood anatomy, but has also been withdrawn by these authors and thus needs no further comments (Johnson & Briggs, 1984).

We are aware that our arrangement of families

can be opposed if emphasis is put on other character complexes, or if most known attributes are simultaneously employed (as attempted by Dahlgren & Thorne, 1984). In our opinion, any so-called conflicting evidence will only strengthen the tissue of intimate relationships between the core families of the Myrtales. If floral and leaf structure for instance point to a Myrtaceous nature of *Psiloxylon*, while the wood witnesses Lythraceous affinities, *Psiloxylon* only bridges a gap between Lythraceae and Myrtaceae; similarly presumed affinities of *Alzatea* with *Crypteronia* (van Beusekom-Osinga & van Beusekom, 1975) in combination with the Lythraceous wood anatomy of *Alzatea*, provides additional evidence of relationships between Melastomataceae and Lythraceae. The main conclusion can only be that whatever minor adjustments one wishes to make in the classification, the 10 core families of the Myrtales, possibly with the addition of Thymelaeaceae, are a very natural assemblage of closely related families.

POSITION OF MYRTALES IN THE DICOTYLEDONS

The hypothesized wood structure of Protomyrtales is a very generalized, primitive type, except for its vestured pits and intraxylary phloem. Among the (super)orders suggested as related to Myrtales in recent systems of classification (Dahlgren, 1980; Takhtajan, 1980; Thorne, 1976; Cronquist, 1981) these two features are absent or very rare and hardly ever occur in combination in Rosiflorae (Rosales, Cunoniales), Corniflorae, Rutiflorae, Theiflorae as shown in Figure 1 (see Dahlgren & Thorne, 1984, for a review of putative relatives and comparison of various attributes of these taxa with Myrtales). Of these only Vochysiaceae pro parte combine vestured pits and intraxylary phloem. This family is wood anatomically specialized (cf. Quirk, 1980) and any affinities to Myrtales can at most be very remote. In Dahlgren's (1980) and Thorne's (1976) system the Myrtiflorae are positioned next to Gentianiflorae in their pictorial "transverse sections through the phylogenetic shrub," but these authors do not comment on mutual affinities between these orders. The anatomical evidence would support a common derivation because the combination of vestured pits and intraxylary phloem is well represented in the order Gentianales. Moreover, primitive features like scalariform perforations occur sporadically in some representatives, fiber-tracheids also oc-

cur, and even the diversity of crystal types including raphides and styloids is matched (cf. Metcalfe & Chalk, 1950); the single family Loganiaceae, if taken in a broad sense, covers much of the wood anatomical diversity also encountered in Myrtales (cf. Mennega, 1980).

If less weight is attached to intraxylary phloem and vestured pits, the primitive Protomyrtalean wood anatomy could be used to argue in favor of affinities with a majority of the larger orders of Dicotyledons, because in most of them there are at least some representatives with scalariform perforations, fiber-tracheids and primitive parenchyma distribution and ray type. In that case the Rhizophoraceae would also be a candidate for affinity (cf. van Vliet's reconstruction of Protorhizophoraceae wood), but it should be stressed here that Rhizophoraceae are not more similar to Myrtales than to many other, unrelated woody Dicotyledons.

With these vague conclusions on the ordinal and supraordinal level we have stretched the possibilities of systematic wood anatomy. With abounding parallelisms partly directed or counteracted by ecological trends (cf. Baas, 1976, 1982; Carlquist, 1975c, 1980), further interpretation of extant wood anatomical diversity patterns with a bearing on events, that must have taken place in early Cretaceous times (cf. Muller, 1981, for the earliest pollen records of Myrtaceae), would be indulging in very wild speculation indeed.

LITERATURE CITED

- AMOS, G. L. 1952. Silica in timbers. C.S.I.R.O. Bull. No. 267.
- BAAS, P. 1973. The wood anatomical range in *Ilex* (Aquifoliaceae) and its ecological and phylogenetic significance. *Blumea* 21: 193-258.
- . 1976. Some functional and adaptive aspects of vessel member morphology. In P. Baas, A. J. Bolton & D. M. Catling (editors). *Wood Structure in Biological and Technological Research*. Leiden Bot. Ser. 3: 157-181. Leiden University Press, The Hague.
- . 1977. The peculiar wood anatomy of *Lepidospermum crassipes* Lehm. (Myrtaceae). I.A.W.A. Bull. 1977/2: 25-30.
- . 1979. The anatomy of *Alzatea* Ruiz & Pav. (Myrtales). *Acta Bot. Neerl.* 28: 156-158.
- . 1982. Systematic, phylogenetic and ecological wood anatomy. History and perspectives. In P. Baas (editor), *New Perspectives in Wood Anatomy*. Martinus Nijhoff/W. Junk, The Hague.
- & E. WERKER. 1981. A new record of vestured pits in Cystaceae. I.A.W.A. Bull. n.s. 2: 41-42.
- & R. C. V. J. ZWEIFPENNING. 1979. Wood anatomy of Lythraceae. *Acta Bot. Neerl.* 28: 117-155.

- BAILEY, I. W. 1933. The cambium and its derivate tissues. VII. Structure, distribution and diagnostic value of vestured pits in dicotyledons. *J. Arnold Arbor.* 14: 259–272.
- BEUSEKOM-OSINGA, R. VAN & C. F. VAN BEUSEKOM. 1975. Delimitation and subdivision of the Crypteroniaceae (Myrtales). *Blumea* 22: 255–266.
- BRIDGWATER, S. D. & P. BAAS. 1978. Wood anatomy of the Punicaceae. *I.A.W.A. Bull.* 1978/1: 3–6.
- BRIGGS, B. G. & L. J. S. JOHNSON. 1979. Evolution in the Myrtaceae. Evidence from inflorescence structure. *Proc. Linn. Soc. New South Wales* 104: 157–256.
- BUTTERFIELD, B. G. & B. A. MEYLAN. 1974. Vestured scalariform perforation plate openings in *Neomyrtus paniculata*. *Austral. J. Bot.* 22: 425–427.
- CARLQUIST, S. 1961. *Comparative Plant Anatomy*. Rinehart & Winston, New York.
- . 1962. A theory of pedomorphosis in dicotyledonous woods. *Phytomorphology* 12: 30–45.
- . 1975a. Wood anatomy and relationships of the Geissolomataceae. *Bull. Torrey Bot. Club* 102: 128–134.
- . 1975b. Wood anatomy of Onagraceae with notes on alternative modes of photosynthate movement in Dicotyledon woods. *Ann. Missouri Bot. Gard.* 62: 386–424.
- . 1975c. *Ecological Strategies of Xylem Evolution*. Univ. of California Press, Berkeley.
- . 1977. Wood anatomy of Onagraceae: additional species and concepts. *Ann. Missouri Bot. Gard.* 64: 627–637.
- . 1980. Further concepts in ecological wood anatomy, with comments on recent work in wood anatomy and evolution. *Aliso* 9: 499–553.
- & L. DEBUHR. 1977. Wood anatomy of Penaeaceae (Myrtales). Comparative, phylogenetic and ecological implications. *Bot. J. Linn. Soc.* 75: 211–227.
- CHATTAWAY, M. M. 1955. Crystals in woody tissues I. *Trop. Woods* 102: 55–74.
- CRONQUIST, A. 1968. *Evolution and Classification of Flowering Plants*. Houghton Mifflin, Boston.
- . 1981. *An Integrated System of Classification of Flowering Plants*. Columbia Univ. Press.
- DADSWELL, H. E. 1972. The anatomy of Eucalypt woods. Forest Products Lab., Div. of Applied Chemistry Technical Paper No. 66; C.S.I.R.O. Australia.
- DAHLGREN, R. M. T. 1980. A revised system of classification of the Angiosperms. *Biol. J. Linn. Soc.* 80: 91–124.
- & R. F. THORNE. 1984 [1985]. The order Myrtales: circumscription, variation, and relationships. *Ann. Missouri Bot. Gard.* 71: 633–699.
- EXELL, A. W. & C. A. STACE. 1966. Revision of the Combretaceae. *Bol. Soc. Brot.* 40: 4–25.
- INGLE, H. D. & H. E. DADSWELL. 1953. The anatomy of the timbers of the south-west Pacific area. III. Myrtaceae. *Austral. J. Bot.* 1: 353–401.
- JOHNSON, L. J. S. & B. G. BRIGGS. 1984 [1985]. Myrtales and Myrtaceae—a phylogenetic analysis. *Ann. Missouri Bot. Gard.* 71: 700–756.
- KRIBS, D. A. 1935. Salient lines of structural specialization in the wood rays of dicotyledons. *Bot. Gaz. (Crawfordsville)* 96: 547–557.
- . 1968. *Commercial Foreign Woods on the American Market*. Dover Publications, New York.
- LOURTEIG, A. 1965. On the systematic position of *Alzatea verticillata*. *Ann. Missouri Bot. Gard.* 52: 371–378.
- MENNEGA, A. M. W. 1980. Anatomy of the secondary xylem. In A. J. M. Leeuwenberg (editor), *Loganiaceae. Die Natürlichen Pflanzenfamilien Ed. 2, 28 b I*: 112–161.
- METCALFE, C. R. & L. CHALK. 1950. *Anatomy of the Dicotyledons*. Clarendon Press, Oxford.
- MEYLAN, B. A. & B. G. BUTTERFIELD. 1974. Occurrence of vestured pits in the vessels and fibres of New Zealand woods. *New Zealand J. Bot.* 12: 3–18.
- & ———. 1978. *The structure of New Zealand woods*. D.S.I.R. Bull. No. 222, Wellington.
- MILLER, R. B. 1977. Vestured pits in Boraginaceae. *I.A.W.A. Bull.* 1977/3: 43–48.
- MOLL, J. W. & H. H. JANSSONIUS. 1918. *Mikrographie des Holzes der auf Java Vorkommenden Baumarten. III*. Brill, Leiden.
- MUJICA, M. B. & D. F. CUTLER. 1974. Taxonomic implications of anatomical studies on the Oliniaceae. *Kew Bull.* 29: 93–123.
- MULLER, J. 1981. Fossil pollen records of extant Angiosperms. *Bot. Rev. (Lancaster)* 47: 1–142.
- QUIRK, J. T. 1980. Wood anatomy of the Vochysiaceae. *I.A.W.A. Bull. n.s. 1*: 172–179.
- RIZZINI, C. T. & P. OCCHIONI. 1949. *Dialypetalanthaceae*. *Lilloa* 17: 244–288.
- SCHMID, R. 1972. A resolution of the *Eugenia-Syzygium* controversy (Myrtaceae). *Amer. J. Bot.* 59: 423–436.
- . 1980. Comparative anatomy and morphology of *Psiloxylon* and *Heteropyxis*, and the subfamilial and tribal classification of Myrtaceae. *Taxon* 29: 559–595.
- TAKHTAJAN, A. L. 1980. Outline of the classification of flowering plants (Magnoliophyta). *Bot. Rev. (Lancaster)* 46: 225–359.
- TAN, K. 1980. Studies in the Thymelaeaceae. I. Notes Roy. Bot. Gard. Edinburgh 38: 149–164.
- THORNE, R. F. 1976. A phylogenetic classification of the Angiospermae. *Evol. Biol.* 9: 35–106.
- . 1981. Phytochemistry and Angiosperm phylogeny. A summary statement. In D. A. Young & D. S. Seigler (editors), *Phytochemistry and Angiosperm Phylogeny*. Praeger, New York.
- VENKATESWARLU, J. & P. S. P. RAO. 1964. The wood anatomy and the taxonomic position of Sonneratiaceae. *Curr. Sci.* 33: 6–9.
- VLIET, G. J. C. M. VAN. 1975. Wood anatomy of the Crypteroniaceae sensu lato. *J. Microscopy* 104: 65–82.
- . 1976a. Radial vessels in rays. *I.A.W.A. Bull.* 1976/3: 35–37.
- . 1976b. Wood anatomy of the Rhizophoraceae. In P. Baas, A. J. Bolton & D. M. Catling (editors), *Wood Structure in Biological and Technological Research*. Leiden Bot. Ser. 3: 20–75. Leiden University Press, The Hague.
- . 1978. The vestured pits of Combretaceae and allied families. *Acta Bot. Neerl.* 27: 273–285.
- . 1979. Wood anatomy of the Combretaceae. *Blumea* 25: 141–223.

- . 1981. Wood anatomy of the palaeotropical Melastomataceae. *Blumea* 27: 395–462.
- , J. KOEK-NOORMAN & B. J. H. TER WELLE. 1981. Wood anatomy and classification of the Melastomataceae. *Blumea* 27: 463–473.
- WELLE, B. J. H. TER & J. KOEK-NOORMAN. 1979. On fibres, parenchyma and intermediate forms in the genus *Miconia* (Melastomataceae). *Acta Bot. Neerl.* 27: 1–9.
- & ———. 1981. Wood anatomy of the neotropical Melastomataceae. *Blumea* 27: 335–394.
- & A. M. W. MENNEGA. 1977. On the presence of large styloids in the secondary xylem of the genus *Henriettea* (Melastomataceae). *I.A.W.A. Bull.* 1977/2: 31–35.